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Phellinus laevigatus s. l. (Hymenochaetales): a ring species

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Abstract: *Phellinus laevigatus* s. l. has evolved as a ring species, which was distributed in Paleocene from the eastern part of Asia via North America to Europe and further to West Siberia. As a result of clinal variation of basidiospores, three allopatric taxa in two species evolved. Of the two species (European–West Siberian *Ph. laevigatus* s. str. and *Ph. betulinus* (Murrill) Parmasto, comb. nova), latter is composed of two subspecies (ssp. *betulinus* and ssp. *orienticus* Parmasto ssp. nova), one distributed in North America and the other in East Asia.

Kokkuvõte: Ringiliik *Phellinus laevigatus* s.l. (Hymenochaetales).

Phellinus laevigatus s.l. (Hymenochaetaceae) on tekkelt nn. ringliik, mis oletatavasti levis paleotseenis parasvöötmes Aasia idaosast üle Põhja-Ameerika Euroopasse ja sealt Lääne-Siberisse. Seoses eoste suuruse klinaalse muutlikkusega kujunes kolm allopatrilist taksonit; kahest liigist (Euroopa–Lääne-Siberi *Ph. laevigatus* s. str. ja *Ph. betulinus* (Murrill) Parmasto, comb. nova) esineb viimane kahe alamliigina (ssp. *betulinus* ja ssp. *orienticus* Parmasto, ssp. nova) – üks neist Põhja-Ameerikas ja teine Ida-Aasias.

INTRODUCTION

Polyporus laevigatus was described by E. Fries in 1874 as a species of his large genus *Polyporus,* in its group V. Resupinati, ** *Poris ferrugineis cinnamomeisve.* Most of the species of this subgroup are now considered to be the resupinate species of the genus *Phellinus* Pat. *P. laevigatus* was combined as *Phellinus laevigatus* (Fr.) by Bourdot & Galzin in 1927; however, their description of the specimens found in France refers to *Ph. rhamni* (M. Bondartseva) Jahn (cf. Jahn, 1967: 89; Niemelä, 1972: 50).

Ito (1955) and some American authors have included *P. laevigatus* as a synonym to *Fomes igniarius* (Lowe, 1957: 56) or as a variety of this species (Overholts, 1953; Baxter, 1934). Closely related North American *Fomitiporella betulina* Murrill, *F. prunicola* f. *betulicola* Peck and *F. ludoviciana* Murrill have been considered to be synonymous with *Ph. laevigatus* by Aoshima (1950: 165), Lowe (1957, 1966), Niemelä (1972) and Kotlaba (1984).

According to most authors who have studied polypores, *Ph. laevigatus* is widely distributed in the temperate zone of the northern hemisphere, mainly on wood of *Betula* spp. (Ryvarden & Gilbertson, 1994; Gilbertson & Ryvarden, 1987; Niemelä, 1972; Núñez & Ryvarden, 2000). The southernmost locality of this species (species complex) has been indicated from subalpine forests of Himalayas in India and Nepal (Sharma, 1995: 155).

No significant differences between the collections from different continents have been indicated by most authors. For example, exactly the same basidiospore size 4–5×3–4 µm has been indicated for specimens from the former Soviet Union (incl. Russian Far East) by Bondarceva (1986), from Poland by S. Domański (1965), from Europe by Ryvarden & Gilbertson (1994), from India by Sharma (1995: 154), from East Asia by Núñez & Ryvarden (2000); 4–6×3.5–5 µm from Ural by Stepanova-Kartavenko (1967), 4.1–5.2×3.1–4 µm from Finland by Niemelä (2005), 4–4.5(–5)×3–4 µm from Germany and Austria by Jahn (1967). Basidiospores are described as a little bit smaller in the North American specimens: 3.5–4.5×2.5–3.5 µm by Lowe (1958) and Lowe & Gilbertson (1961), 3.5–4.5×3–4 µm by Overholts (1953), 3–4×2.5–3 µm by Lindsey & Gilbertson (1978). Pore size has been described smaller in North American specimens (8–10 per mm) than in the European ones (5–8 per mm); in Chinese specimens, it has been given as (6–)7–9(–10) per mm (Zhang, Dai & Zhou, 2005), but 6–7 per mm by Teng (1964).

The specimens collected in Australasia and described by Cunningham (1965) as *Fuscoporia (= Phellinus) laevigata* are different from the

European ones, and were collected on trees of several families but not of Betulaceae. Identity of the small-spored (3.8–4.7×3.2–4 µm) *Ph. laevigatus* found in Papua New Guinea on *Coffea* spp. and unidentified angiospermic trees (Quanten, 1997: 277) is unknown.

The author of this paper found that all specimens of *Ph. laevigatus* collected in East Siberia and Russian Far East have distinctly smaller basidiospores than the European ones. Parmasto (1985) described (without a Latin diagnosis) the temperate Asian Far East population of *Ph. laevigatus* as an independent closely related species *Ph. orienticus.* Dai (1996: 96) found, that the specimens collected by him in China are identical with this new taxon; mean basidiospore size of these is 3.27×2.66 µm (n = 5). He found, that North American specimens are in between the European and NE Asian materials, and therefore refrained from adopting the name *Ph. orienticus* (Dai, 1999: 48). Basidiopores of the Chinese specimens were later described as 3–4(–4.5)×2.1–3.1 µm by Zhang, Dai & Zhou (2005). *Ph. orienticus* was accepted as a distinct taxon only by Wagner & Fischer (2002); they found in their study on molecular phylogeny of *Phellinus* s. l. and *Inonotus* s. l., that *Ph. laevigatus* and *Ph. orienticus* form a subclade in the MP tree based on nuc-lsu rDNA sequences, supported by 86% bootstrap value. The difference between the sequences of the two species used for their study is small (4 different bases) but is a consistent difference (GenBank, AF311034 and AY059017).

The aim of this paper is to characterize the variation of the morphological characters of this species complex (or possibly of one, variable species) in Asia, North America, Europe and Australasia, and to evaluate taxonomically the differences between these populations (or taxa). For comparison, several specimens of related species *Ph. prunicola, Ph. rhamni* and *Ph. spiculosus* were studied as well. All species of the *Ph. laevigatus* group are characterized by resupinate basidiomata, presence of hymenial setae, broadly ellipsoid or subglobose hyaline non-dextrinoid basidiospores, and all grow on angiospermic substrata.

MATERIALS AND METHODS

Spore and setal measurements were made with the aid of a Sony CCD Video Camera attached to a Nikon Labophot 2 microscope and analysed by Global Lab Image (Data Translation Inc., Marlboro) software; 30 basidiospores and 15 setae were measured in each specimen. 90%-expected tolerance limits of specimen means were calculated as described by Parmasto & Parmasto (1987, pp. 108–112). For statistical comparisons (ANOVA, Mann–Whitney U-test), a free trial program Analyse-it for Microsoft Excel (Analyse-it Software, Ltd, UK) was used. Numerical taxonomy and multivariate analyses were performed using the program NTSYSpc Vers. 2.2 (Exeter Software, 2005). Herbarium acronyms are after Holmgren et al. (1990).

RESULTS

Distribution and hosts of taxa, variation of characters

Phellinus orienticus Parmasto *nom. subnudum,* Proc. Indian Acad. Sci. (Plant Sci.) 94 (2 & 3): 375. 1985.

This taxon has been collected in Russian Far East – in Kamtchatka, southernmost part of Sakha (Yakutia), in Amur Reg. and Jewish Autonomous Reg., in Khabarovsk and Primorsk Territories, on Sakhalin and in Kurile Islands (Iturup Is.); it has also been found in Japan and China. The westernmost locality is in Central Siberia (near Krasnoyarsk, 55°55'N, 92°45'E). In China, *Ph. laevigatus* s. l. (possibly the small-basidiospore taxon called *Ph. orienticus* here) has been found in Guangxi, Hainan, Hebei, Heilongjiang, Hunan, Jilin, Ningxia, Shaanxi and Sichuan provinces (Teng, 1964; Tai, 1979; Zhang, Dai & Zhou, 2005).

Ph. orienticus has been found on several species of *Betula: B. costata, B. dahurica, B. ermanii, B. lanata, B. mandshurica, B. maximowicziana* and *B. paraermanii.*.

Thirty-one specimens were studied; 90%-expected tolerance limits of specimen mean size is: basidiospores 3.02–4.23×2.48–3.07 µm, Q = 1.11–1.51 (species means: 3.62×2.78 µm, Q = 1.31), setae 14.7–17.6×4.7–5.7 µm, Q = 2.8–3.5 (species means: 16.13×5.18 µm, Q = 3.11), pores 6.2–8.4 per mm (species mean: 7.31). No clinal gradations in morphological characters were found between the Kamtshatkan, Kurilian, Russian Far East and Central Siberian populations.

See also *Ph. betulinus* (Murrill) Parmasto below.

Phellinus betulinus (Murrill) s.str. (American specimens)

I have seen 56 specimens of *Ph. betulinus* (30 of these were with basidiospores), collected in Canada (British Columbia, Newfoundland, Nova Scotia, Ontario, Québec) and in the USA (Georgia, Idaho, Louisiana, Maine, Maryland, Michigan, Missouri, Montana, New Hampshire, New York, North Carolina, Pennsylvania, Tennessee, Vermont, Washington, West Virginia, Wisconsin and Wyoming States) on *Betula* spp.: *B. alba, B. alleghaniensis, B. fontinalis, B. lenta, B. lutea, B. nigra, B. occidentalis, B. papyrifera* and *B. populifolia.* Holotype of *Fomitiporella betulina* Murrill has been studied: Maine, N. slopes of Boarstone Mt., Willimantia, Piscataquis Co., on birch, W.A. Murrill 2511, Sept. 12–14, 1905 (NY); it was also studied by Lowe (1966) and Niemelä (1972) already who synonymized it with *Ph. laevigatus*.

In the N. American herbaria, several specimens have been misidentified as *Ph. (F.) betulinus* or *Ph. (F.) laevigatus;* these are *Phellinus alni* (Bondartsev) Parmasto, *Ph. inermis* (Ell. & Everh.) G. Cunn., *Ph. johnsonianus* (Murrill) Ryvarden, *Ph. lundellii* Niemelä, *Ph. punctatus* (Fr.) Pilát, *Ph. prunicola* (Murrill) Gilbertson, *Ph. robustus* (P. Karst.) Bourdot & Galzin, *Ph. spiculosus* (Campbell & Davidson) Niemelä, *Ph. tremulae* (Bondartsev) Bondartsev & Boriss. and *Ph. vaninii* Ljub.

Thirty specimens were studied; 90%-expected tolerance limits of specimen mean size is: basidiospores 3.96–4.40× 2.84–3.64 µm, Q = 1.18–1.42 (species means: 4.18×3.22 µm, Q = 1.30), setae 13.2–18.6×5.3–6.8 µm, Q = 2.1–3.3 (species means: 15.91×6.00 µm, Q = 2.68), pores 6.8–9.5 per mm (species mean: 8.18). No clinal gradations in morphological characters were found between the western and eastern or other local populations.

Phellinus betulinus (Murrill) Parmasto comb. nova – Basionym: *Fomitiporella betulina* Murrill, North Amer. Flora 9: 12. 1907. – MB 511114.

In the chapter "Discussion" of this paper, it will be concluded, that it is better to distinguish East Asian *Ph. orienticus* ad int. and North American *Ph. betulinus* from each other not as independent species, but as morphologically close allopatric subspecies. The characters' variation of the joint dataset may be generalized as follows:

Sixty-one specimens were studied; 90%-expected tolerance limits of specimen mean size is: basidiospores 3.25–4.55×2.51–3.49 µm, Q = 1.14–1.47 (species means: 3.90×3.00 µm, Q = 1.30), setae 13.9–18.1×4.7–6.5 µm, Q = 2.3–3.0 (species means: 16.02×5.59 µm, Q = 2.90), pores 6.3–9.1 per mm (species mean: 7.74). Basidiospores always thin-walled.

Two subspecies are distinguished here: North American **ssp. betulinus** (described above as *Ph. betulinus* s. str., American specimens), and

Phellinus betulinus ssp. orienticus Parmasto ssp. nova – MB 511115.

Syn.: *Ph. orienticus* Parmasto nom. subnud. – Sporae late ellipsoideae, tenuiter tunicatae, magnitudo media speciminum 3.25–4.55×2.51–3.49 µm. Holotype: Russia, Primorsk Terr., Distr. Ternei, Sikhote-Alin Nature Reserve, Chanov Rivlet, on a fallen trunk of *Betula mandshurica,* 19 Sep 1976 E. Parmasto (TAA 52831; isotypes: BPI, H, K, LE). – Mean size of the basidiospores: 3.25–4.55×2.51–3.49 µm. – In the holotype mean size of basidiospores is 3.29×2.70 µm (*Q* = 1.22), of setae – 16.2×4.8 µm; 8 pores per mm.

Phellinus laevigatus (Fr.) Bourdot & Galzin, Hyménom. France 624. 1928. – *Polyporus laevigatus* Fr., Hymen. Europ. 571. 1874.

I have seen more than 150 collections from Europe, West Siberia and Middle Asia. The species is uncommon in North and East Europe, rare in Central and southern, absent in western Europe; its easternmost locality is in the Krasnoyarsk Territory in Central Siberia (Taseyevo, 57°13'N, 94°54'E), southeastern localities are in Khakasia (Sayani Mts., 53°15'N, 91°67'E), Tajikistan (Pamir Mts.) and Uzbekistan (E of Tashkent).

The main hosts for this fungus are *Betula pendula* and *B. pubescens,* rarely *B. celtiberica* and *Alnus glutinosa.* Bondartseva (1986) mentioned also *Frangula alnus, Quercus* and *Salix,* Ryvarden & Gilbertson (1994) *Acer, Corylus, Fagus, Fraxinus, Salix* and *Sorbus,* but I have not seen any specimens from these substrata; *F. alnus* is a substrate for *Ph. rhamni* in Austria (Jahn, 1967: 87, 90). Doğan & Öztürk (2006: 203) indicated a locality of *Ph. laevigatus* in South Central Turkey (Karaman Prov.) on *Populus* sp., but this may be a misidentified specimen.

Thirty-two specimens were studied; 90%-expected tolerance limits of specimen mean size is: basidiospores 4.56–5.46×3.58–4.15 µm, Q = 1.21–1.39 (species mean: 5.01×3.87 µm, Q = 1.30), setae 14.4–21.1×5.3–6.5 µm, Q = 2.4–3.6 (species mean: 17.75×5.89 µm, Q = 3.03), pores 5.8–8.4 per mm (species mean: 7.11). Basidiospores usually had slightly thickened walls. No clinal gradatations in morphological characters were found between the Norwegian, Estonian, Uzbekistan and Central Siberian populations.

Fuscoporella (= Phellinus) **ludoviciana** Murrill, North Amer. Flora 9: 9. 1907.

The holotype, the only known specimen of this species (USA, La, St Martinsville P.O., 11 Mar 1889 A.B. Langlois 1737 (NY)) was studied by Lowe (1966) and Niemelä (1972) and synonymized with *Ph. laevigatus*. I have restudied it; mean size of 30 basidiospores is 4.56×3.91 µm, *Q* = 1.16; setae (n = 15) 16.6×7.3 µm; pores 7 per mm; pore surface colour is 7.5 YR 5.5/4 in the Munsell book of color (1976). A similar specimen has been found in USA, Maine on *Betula alba* (MICH Baxter 1-4226g I) and identified as *Poria laevigata* by D.V. Baxter; it has basidiospores 5.38×4.28 µm, setae 18.0×6.1 µm and pores 7.5 per mm. According to these data, these two specimens seem to be similar to if not identical with the European *Ph. laevigatus*. To clarify the question, more specimens of this fungus must be collected and studied.

Phellinus prunicola (Murrill) Gilbertson, Mycotaxon 9: 73. 1979. – *Fomitoporia prunicola* Murrill, North Amer. Flora 9: 9. 1907.

In addition to the distribution data indicated by Gilbertson & Ryvarden (1987: 595–596),this species is found also in Canada, Ontario, at Lake Temagami (21 Jun 1933 L.O. Overholts. TRTC 4927) and Upper Island Lake (6 Oct. 1970 J. Ginns 1523; DAOM 137869), and in several localities in the Michigan, New Hampshire, New York and Tennessee States (MICH, PAC, TENN, TRTC); specimens seen have been found on *Prunus pennsylvanica, P. serotinus* and *Prunus* sp. *Ph. betulinus* differs from this species in smaller basidiospores, less slender setae and other substrata.

7 specimens were studied; specimen mean size is: basidiospores 5.21–6.43×3.86–4.63 µm, Q = 1.30–1.44, setae 16.0–21.8×4.5–6.8 µm, Q = 2.6–4.6, pores 6–9.5 per mm.

Phellinus rhamni (M. Bondartseva) H. Jahn, Westfäl. Pilzbriefe 6 (3–6): 89. 1967. – *Phellinus laevigatus* f. *rhamni* M. Bondartseva, Notulae Syst. Sect. Cryptog. Inst. Bot. V.L. Komarovii Acad. Sci. URSS 13: 230.

This is found in Central and southern Europe (incl. southern European Russia and Chechnya) and in Kazakhstan on *Rhamnus* spp., rarely also on *Paliurus, Frangula alni* and several woody species of Ericaceae and Papilioniaceae.

Types studied: 1) Kazakhstan Republic, Burlinsk region at the Ural River, J.V. Sinadsky 1956 (LE, holotype); 2) Russia, Bryansk Reg., Bryansk Experimental Forest Division, A.S. Bondartsev 1932 (LE; paratype, but indicated as lectotype on the label by M.A. Bondartseva). – Pores about 6 per mm, pore layer deeply creviced. Setae ventricose, with conical tip, (18–)20–30×(6–)7.5–10 µm (mean of 15 setae: 23.8×8.2 µm, Q = 2.9). Basidiospores 5.3–6.0(–6.3)×(4.2–)4.5–5.3 µm.

Four specimens were studied; specimen mean size is: basidiospores 5.46–5.78×4.22–4.82 µm, Q = 1.17–1.30, setae 17.2–30.2×7.7–8.4 µm, Q = 2.8–3.4, pores 6–7 per mm.

Clearly distinct from *Ph. laevigatus* s. l. in basidiospores 4.5–6×4–5 µm; however, this character was not mentioned by Sinadsky & Bondartzeva (1960) in the original description of the species. They described the species as having tubes in only one layer; however, the paratype and a specimen collected by us in Chechnya are actually with 3–4 tube layers.

Phellinus spiculosus (Campbell & Davidson) Niemelä, Ann. Bot. Fenn. 9: 57. 1972. – *Poria spiculosa* Campbell & Davidson, Mycologia 34: 17. 1942.

Found in western and southwestern USA, mainly on *Quercus* sp. and *Carya glabra,* also on *Acer saccharum* and *Persea* sp. In addition to the localities, mentioned by Gilbertson & Ryvarden (1987), found also in Illinois, Indiana, Missouri and Ohio, and in Canada (Ontario, York Co.) (SYRF, PAC, NY, MICH). *Ph. betulinus* differs in smaller basidiospores and other substrata,

Sixteen specimens were studied; 90%-expected tolerance limits of specimen mean size is: basidiospores 4.99–6.10×3.83–5.23 µm, Q

= 1.10–1.36 (species mean: 5.54×4.53 µm, Q = 1.23), setae 14.1–22.1×5.5–8.7 µm, Q = 2.1–3.1 (species mean: 18.13×7.12 µm, Q = 2.58), pores 5.2–9.1 per mm (species mean: 7.13).

Phellinus sublaevigatus (Cleland & Rodway) P.K. Buchanan & Ryvarden, Austral. Syst. Bot. 6: 230. 1993. – *Poria sublaevigata* Cleland & Rodway, Pap. Roy. Soc. Tasm. 1928: 39. 1928. – *Poria brunneo-adhaerens* Cleland & Rodway, Pap. Roy. Soc. Tasm. 1928: 42. 1928. – *Fuscoporia laevigata* (Fr. s. G. Cunn.) G. Cunn., Bull. New Zeal. Dept. Sci. Industr. Res., Pl. Dis. Div. 73: 9. 1948.

Description of *Fuscoporia (= Phellinus) laevigata* by Cunningham (1965: 210) is different from the European specimens: setae are longer, pores and basidiospores larger. Moreover, the New Zealand, Australian and Tasmanian specimens have different hosts belonging to the families Cunoniaceae, Lauraceae, Monimiaceae, Myrtaceae or Rubiaceae but never to Betulaceae.

We studied 12 Australasian specimens of this fungus from the herbarium PDD, identified by G.H. Cunningham as *Ph. laevigatus* or *Poria brunneo-adhaerens* (incl. its iso-lectotype PDD 3481). All these belong to *Ph. sublaevigatus* (see http://nzfungi.landcareresearch.co.nz/html/mycology.asp and select *Herbarium*). Most of the specimens are devoid of basidiospores; PDD 11158 has a few, mostly deformed basidiospores 6.5–7×4.4–5.8 µm; PDD 5504 had 12 basidiospores with mean size 5.12×4.11 µm, *Q* = 1.25; basidiospores are weakly to strongly dextrinoid. Mean size of setae is 23–32×3.7–5.1, pores are in all specimens about 6 per mm. Buchanan & Ryvarden (1993: 230) described the basidiospores of *Ph. sublaevigatus:* with thickened and dextrinoid or thick and strongly dextrinoid walls, 6.5–7×5–6 (holotype) or 6–6.5×4.5–5.5 µm (HO 104195). According to these data, the species does not belong to the *Ph. laevigatus*-group.

Comparison of statistical data

Using analysis of variance (ANOVA) and Mann–Whitney U-test, differences between means or medians of basidiospore, setal and pore measurement data given in the Appendix to this paper were studied in the three possible species, earlier joined under the name *Ph. laevigatus* (sensu lato). Results of the comparison are given below.

Phellinus orienticus/*Ph. betulinus* s. str.: basidiospore length, basidiospore width, setae width, setal quotient and number of pores per mm – difference significant on 0.001 level (ANOVA, Mann–Whitney U-test); basidiospore form (*Q*) and setal length – difference insignificant.

Phellinus betulinus s. str./*Ph. laevigatus* s. str.: basidiospore length, basidiospore width, setal length, setal quotient and number of pores per mm - difference significant on 0.001 level (ANOVA, Mann–Whitney U-test); basidiospore form (*Q*) and setal width – difference insignificant.

Phellinus betulinus s. l. (*Ph. orienticus* + *Ph. betulinus* s. str.)/*Ph. laevigatus* s. str.: basidiospore length, basidiospore width, setal length, number of pores per mm – difference significant on 0.001 level; setal width – difference significant on 0.005 level (ANOVA, Mann–Whitney U-test); basidiospore form (*Q*) – difference significant on 0.001 level (U-test) or insignificant (ANOVA); setal quotient – difference insignificant.

Basidiospore length is moderately invariable or normally variable, spore width is normally variable in all three taxa (*Ph. orienticus, Ph. betulinus* s. str., *Ph. laevigatus* s. str.). In *Ph. laevigatus* s. l. (i.e., when all three taxa are included to one species), coefficient of variation (CV) of spore length and width is 15% – these measurements are extremely variable. This is a sensitive indicator of possible heterogeneity of the (statistical) sample – cf. Parmasto & Parmasto, 1987: 91–94.

Phenetic analysis

When mean spore size and mean setal size data were used in phenetic analyses, three distinct clusters were found in a dendrogram when average Manhattan distances and complete-link clustering method was used. The three clusters correspond to the groups of specimens collected in East Asia, North America, and Europe plus West Asia, i.e. to the two subspecies of *Ph. betulinus* and *Ph. laevigatus* s.str. The North American cluster is somewhat more similar to the European one than to the East Asian one. Use of other phenetic methods (Euclidean and squared Euclidean distances, unweighted pair-group clustering method, UPGMA) resulted in a clearly distinct European–West Asian group (*Ph. laevigatus* s. str.) and not very distinct clusters of other specimens. When principal

component analysis was used and specimen points presented in a 2- or 3-dimensional plot, two groups are distinctly formed – one for the East Asian–North American taxon and another for the European–West-Asian one.

DISCUSSION

According to the spore measurements of the *Betula*-specialized circumboreal fungus *Ph. laevigatus* s. l, there are three closely related but distinct groups (species, subspecies or populations) with different or only slightly overlapping spore characters. It may be a case of taxonomic speciation by clines, as described by Huxley (1939). According to his views (p. 113), "character-gradations or clines constitute a[nother] type of group-differentiation " of subspecies.

Ring species is a term used mainly in ornithological studies. Stanley (1979: 54) defined it as "a circular chain of partly intergrading subspecies". Irwin et al. (2001) have shown, how small changes can lead to species-level differences, in which reproductively isolated forms are connected by a chain of intermediate populations. The morphological difference between extreme forms is obviously caused by clinal variation; migration is supposed to result in geoclines and arising geographically limited subspecies – or species (Huxley, 1939). Ring species is a special case of *superspecies* as Mayr renamed Rensch's *Artenkreis* in 1931: a monophyletic group of geographically vicariant populations, the members of which have been isolated sufficiently long to have reached species level (Mayr, 1982: 291).

Takhtayan (1970: 65) asserted, that the most ancient species of *Betula* have been found in the Himalayas, in Assam and East Asia. Chen et al. (1999) declared, that the family Betulaceae has originated in Paleocene in Eastern Asia, in the so-called Central China. It may be hypothesized, that the ancestor of *Ph. laevigatus* s. l. had its origin in the same region in Paleocene or Eocene. Dry-land dispersion of East Asian species of living beings west (to Europe) was prevented by the broad Turgai Sea (Turgay Strait, Obik Sea) from the Mid Jurassic (180 Mya) already (Sanmartín et al., 2001), but spreading eastwards was possible from Cretaceous to Late Pliocene and Pleistocene – through Beringia (over Beringian Land Bridge) to North America. Macrofossils of *Betula* have been found in the middle Eocene of North America (Crane & Stockey, 1987) about 48 Mya (Chen et al., 1999). Dillhoff et al. (2005) found, that *Betula* was common in the Early Middle Eocene forests in Okanagan Highlands in British Columbia (Canada).

Eastward dispersal was predominating in the Nearctic during the Tertiary. Trans-Atlantic land bridges joining eastern North America, Greenland, Faeroes and Europe persisted until Early Eocene (50 Mya, *Thulean Bridge*) and until the Late Eocene (39 Mya, *De Geer Bridge*) (Sanmartín et al., 2001). Westward distribution was hindered by the Turgay Strait which split Siberia from North to South until about 30 Mya in Oligocene (Vinogradov, 1967; Tiffney, 1985). It was a broad barrier to migration of species. In Pliocene, East Siberia was covered with step and forest-step vegetation (Vinogradov, 1967); during the Late Pliocene–Pleistocene, the West-Siberian dry continental climate barrier periodically interrupted exchange of biota between Asia and Europe (cf. Sanmartín et al., 2001: 350–351).

According to these paleogeographic data, the *Ph. laevigatus*-complex has had trans-Beringian and trans-Atlantic dispersal in Laurasia. Possibly the ancestral *Ph. laevigatus* dispersed westwards until the Turgai Sea, and in early Eocene eastwards via the Beringian Land Bridge in boreal forests to North America, then via the Thulean Land Bridge to North Europe an then to West Siberia and Middle Asia. Before the ending of the Thulean Bridge, the climate was about the same there as is found in the Scandinavian birch belt today (Dahl, 1963: 186), i.e., suitable for the wood-rotting fungi of the *Ph. laevigatus* group. After cessation of the Trans-Atlantic Land Bridge about 40–50 Mya (Graham, 1999) and Beringian Land Bridge in the beginning of Pliocene about 5 Mya, the area of the ancient ring species *Ph. laevigatus* s. l. was finally split into three parts, and three vicariant taxa with disjunct areas have developed in isolation from one another. As seen from the statistical comparison and phenetic analysis described above, the morphological differences between the three taxa are small but distinct.

When *Ph. laevigatus* and *Ph. betulinus* ssp. *orienticus* growing on the same substrate (birch wood) met afterwards in Central Siberia, neither of the sibling species crossed the contact zone, nowhere they have been found growing together (G.F. Gause's competitive exclusion principle!),

and no "intermediate forms" have been found in that region.

In the genus *Phellinus* s. l., the *Ph. laevigatus* species complex seems to be a "classical" example of allopatric speciation. Among other sibling species in this group of fungi (*Phellinus igniarius*-group), sympatric (ecological) speciation seems to be the main pathway. It is possible, that the European *Ph. rhamni* (on *Rhamnus* spp.) and *Ph. laevigatus* s. str. have diverged from a common ancestor as a result of sympatric speciation. Similar sympatric origin of North American *Ph. prunicola* (on *Prunus* spp.) and *Ph. spiculosus* (mainly on *Carya* and *Quercus* spp.) and *Ph. betulinus* is equally possible but needs further studies.

Another problem is how to rank the three vicariants of the *Ph. laevigatus* 'superspecies', as species or subspecies; it depends on the authors' species concept. In our case a compromise is proposed, to name more similar to each other East Asian and North American taxa as subspecies of *Ph. orienticus,* and to distinguish *Ph. laevigatus* s. str. as an independent species.

CONCLUSIONS

In the group of taxa *Phellinus laevigata* s. lato, two species may be distinguished: *Ph. laevigatus* (Fr.) Bourdot & Galzin s. str and *Ph. betulinus* (Peck) Parmasto with two subspecies: ssp. *betulinus* in temperate North America and ssp. *orienticus* Parmasto in temperate East Asia. Origin of these taxa may be interpreted as evolving a *ring species* from East Asia in Paleocene, which migrated eastwards via North America and Europe to Central Siberia, where *Ph. laevigatus* s. str. met with *Ph. betulinus* ssp. *orienticus*. The three allopatric taxa differentiated from each other after cessation of Beringian and Thulean Land Bridges.

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Appendix. Mean basidiospore length, basidiospore width and their quotient; mean setal length, setal width, their quotient, and mean number of pores per mm in the specimens studied; locality of the collection, and herbarium data.

Phellinus betulinus ssp. orienticus

2.87	2.41	1.19	14.1	5.4	2.6	8	Russia, Primorsk Terr., TAA 59315
3.00	2.53	1.19	15.2	5.4	2.8	6.5	Russia, Sakha Rep., TAA 42098
3.04	2.62	1.16	15.7	4.7	3.3	8	Russia, Primorsk Terr., TAA 47652
3.12	2.66	1.18	15.1	4.9	3.1	8	Russia, Primorsk Terr., TAA 47342
3.29	2.70	1.22	16.2	4.8	3.4	8	Russia, Primorsk Terr., TAA 52831, **holotype**
3.31	2.80	1.19	15.9	5.9	2.7	7	Russia, Kamtshatka Reg., TAA 12464
3.32	2.52	1.32	17.4	5.6	3.1	8	Russia, Primorsk Terr., TAA 100075
3.33	2.87	1.16	17.1	5.3	3.2	8	Russia, Khabarovsk Terr., TAA 104449
3.42	2.69	1.29	17.2	5.1	3.4	6.5	Russia, Primorsk Terr., TAA 76-10
3.43	2.84	1.21	16.3	5.2	3.1	6	Russia, Primorsk Terr., TAA Uss 75-1
3.43	2.89	1.19	15.6	5.0	3.1	6.5	Russia, Primorsk Terr., TAA Uss 75-7
3.44	2.80	1.24	15.5	4.9	3.2	7.5	Russia, Primorsk Terr., TAA 101830
3.46	3.01	1.15	17.0	5.0	3.4	8	Russia, Primorsk Terr., TAA 52720
3.50	2.92	1.20	16.1	4.8	3.3	7.5	Russia, Primorsk Terr., TAA 59630
3.71	2.85	1.30	17.9	5.4	3.3	7	Russia, Sakhalin Is., TAA 102508
3.74	2.62	1.43	15.6	4.9	3.2	7.5	Russia, Primorsk Terr., TAA 59854
3.75	2.84	1.32	15.5	5.0	3.1	7.5	Russia, Primorsk Terr., CHAB 4009
3.79	2.59	1.46	15.4	5.1	3.0	7	Russia, Primorsk Terr., TAA 59849
3.82	2.88	1.32	16.3	5.4	3.0	7	Russia, Primorsk Terr., TAA 112958
3.83	2.70	1.42	16.8	4.9	3.5	7	Russia, Krasnoyarsk Terr., TAA 1971/506
3.83	2.77	1.38	16.0	5.3	3.0	7.5	Russia, Khabarovsk Terr., TAA 104450
3.83	2.99	1.28	16.0	5.3	3.0	7.5	Russia, Kuril Islands, Iturup Is., TAA 96503
3.90	2.60	1.50	15.8	5.2	3.0	7.5	Russia, Sakhalin Is., TAA 47227
3.95	2.87	1.38	17.7	5.7	3.1	7.5	Russia, Primorsk Terr., TAA 101903
3.99	2.61	1.53	16.7	5.2	3.2	8	Russia, Primorsk Terr., TAA 101912
3.99	2.63	1.52	15.0	4.9	3.1	7.5	Russia, Primorsk Terr., TAA 101903
3.99	3.04	1.32	16.2	5.4	3.0	6	Russia, Primorsk Terr., TAA 101579
4.03	3.13	1.29	15.8	5.4	2.9	6.5	Russia, Primorsk Terr., TAA 101724
4.04	2.99	1.36	15.9	5.1	3.1	8	Russia, Primorsk Terr., TAA 102644
4.06	2.78	1.46	17.2	5.5	3.1	7	Russia, Primorsk Terr., TAA 102649
4.10	2.90	1.41	15.7	5.0	3.1	7	Russia, Primorsk Terr., TAA 102667
3.62	2.78	1.31	16.1	5.2	3.1	7.3	Species mean
10%	6%	9%	5%	6%	6%	8%	CV

Phellinus betulinus s. str.

4.02	3.29	1.22	15.7	6.8	2.3	8	Canada, British Columbia, PAC 14037
4.03	3.14	1.29	15.8	6.6	2.4	9	USA, Maine, NY 2511, **holotype** of *Fomitoporella betulina*
4.04	3.05	1.33	17.9	5.6	3.2	7.5	USA, Vermont, DAOM 31763
4.04	3.41	1.18	18.2	6.5	2.8	7	USA, Montana, MICH Baxter 22754-Q
4.07	3.16	1.29	15.1	6.4	2.3	7	USA, New York, PAC, Herb. Overholts 5538
4.07	3.28	1.24	14.9	6.0	2.5	9	USA, New Hampshire, PAC 5025
4.09	2.98	1.37	16.9	5.6	3.0	9	USA, New York, CFMR MJL-528
4.10	3.28	1.25	14.7	6.2	2.4	8	USA, Idaho, PAC 22576
4.11	3.02	1.36	16.4	5.4	3.0	8.5	Canada, Nova Scotia, DAOM 30393
4.11	3.25	1.27	17.0	6.4	2.7	9.5	USA, Washington, PAC 9925
4.12	3.01	1.37	14.6	5.6	2.6	8	Canada, Nova Scotia, DAOM 30095

4.12	3.34	1.24	15.8	6.0	2.7	8	USA, New Hampshire, PAC, Overholts 4565
4.13	3.07	1.34	17.7	5.8	3.1	8.5	Canada, British Columbia, DAOM 22998
4.14	3.09	1.34	13.8	6.0	2.3	8	Canada, British Columbia, DAOM 23000
4.15	3.23	1.28	14.7	6.0	2.5	9	USA, Pennsylvania, PAC 14468
4.16	2.84	1.47	17.8	5.6	3.3	7	Canada, Ontario, DAOM 142069
4.16	3.02	1.38	18.3	5.7	3.2	8	USA, Pennsylvania, CFMR FP-56498
4.16	3.26	1.27	14.4	5.1	2.8	9.5	USA, Wisconsin, MICH Baxter 2-2740
4.16	3.38	1.23	14.3	6.4	2.3	8	USA, New Hampshire, PAC, Overholts 5013
4.19	2.91	1.44	18.4	6.1	3.0	9.5	USA, Montana, CFMR RLG-5835
4.20	3.35	1.25	15.4	6.4	2.4	8.5	USA, New Hampshire, PAC 4940
4.21	3.17	1.33	13.8	5.9	2.4	8	USA, North Carolina, TENN 23420
4.23	3.30	1.28	14.0	5.8	2.4	8	USA, Pennsylvania, PAC 13353
4.27	3.05	1.40	19.0	6.4	3.0	9	USA, Montana, MICH Bennett 400
4.28	3.29	1.30	16.6	5.1	3.3	8	USA, New Hampshire, CFMR FP-125082
4.29	3.44	1.25	14.8	5.8	2.6	7.5	USA, Maine, PAC Marshall 24 May 1933
4.40	3.57	1.23	16.9	6.6	2.6	7.5	USA, Pennsylvania, PAC Overholts 1933
4.41	3.52	1,25	14.4	6.4	2.3	8.5	Canada, Ontario, PAC 14131
4.44	3.54	1.25	15.0	5.9	2.6	6.5	USA, Pennsylvania, PAC Campbell 6 Feb 1934
4.54	3.49	1.30	15.1	6.0	2.5	8	USA, Pennsylvania, PAC Overholts 17359
4.18	3.22	1.30	15.9	6.0	2.7	8.2	Species mean
3%	6%	5%	10%	7%	12%	10%	CV

Phellinus betulinus (Ph. orienticus + Ph. betulinus s. str.)

3.90	3.00	1.30	16.0	5.6	2.9	7.7	Mean
10%	10%	7%	8%	10%	12%	11%	CV

Phellinus laevigatus s. str.

4.43	3.57	1.24	17.1	5.7	3.0	8	Estonia, TAA 46950
4.50	3.81	1.18	17.5	6.0	2.9	8	Russia, Tatarstan, 1977, TAA 77-38
4.57	3.77	1.21	16.3	5.5	3.0	8	Russia, Krasnoyarsk Terr., LE 1964
4.67	3.59	1.31	17.4	6.2	2.8	8	Estonia, TAA 112714
4.69	3.66	1.28	17.1	5.9	2.9	7	Estonia, TAA 53000
4.74	3.90	1.22	18.3	6.1	3.0	6.5	Russia, Siberia, Khakasia Rep., LE 27
4.79	3.74	1.28	16.7	5.5	3.0	8.5	Russia, Siberia, E of Krasnoyarsk, TAA 6938
4.83	3.81	1.27	17.7	6.2	2.9	8	Russia, Siberia, Khakasia Rep., TAA 9189
4.83	3.82	1.26	19.2	5.7	3.4	8	Russia, Perm Reg., TAA 104224
4.85	3.79	1.28	18.6	5.4	3.5	6.5	Russia, Siberia, Khakasia Rep., Mts., TAA 9150
4.86	3.73	1.30	17.2	5.7	3.0	7	Russia, W Siberia, Tyumen Reg., TAA 17112
4.86	3.79	1.28	18.9	6.8	2.8	6	Estonia, TAA 2235
4.88	3.68	1.33	17.0	5.7	3.0	7	Estonia, TAA 100231
4.91	3.84	1.28	17.6	5.9	3.0	8	Estonia, TAA 2545
4.92	3.93	1.25	16.4	6.1	2.7	8	Russia, Siberia, Khakasia Rep., TAA 8986
4.97	3.94	1.26	17.4	5.7	3.1	7	Russia, Tatarstan, TAA 100861
5.00	3.91	1.28	15.7	5.7	2.8	6.5	Estonia, TAA 104235
5.00	3.91	1.28	22.0	5.8	3.8	8	Estonia, TAA 55722
5.01	3.65	1.38	17.1	6.1	2.8	6	Estonia, TAA 17739
5.06	3.91	1.29	18.1	5.9	3.1	7.5	Estonia, TAA 2358
5.06	3.97	1.28	15.7	5.4	2.9	7.5	Estonia, TAA 40438
5.13	3.85	1.33	19.6	5.8	3.4	6	Tajikistan, Pamir Mts., TAA 97339
5.18	3.93	1.32	16.9	5.7	3.0	7.5	Estonia, TAA 104373
5.20	4.47	1.16	13.8	6.5	2.1	6	Sweden, PAC, Overholts 5975
5.22	3.81	1.37	16.4	5.6	3.0	7	Estonia, TAA 2537

5.24	4.02	1.30	17.1	5.8	2.9	7	Estonia, TAA 54897
5.25	4.03	1.30	16.8	5.3	3.2	7	Estonia, TAA 3054
5.29	3.87	1.37	15.1	6.5	2.3	7	Norway, O 2848
5.29	3.94	1.34	18.6	6.1	3.0	6.5	Estonia, TAA 105301
5.29	3.94	1.34	17.4	6.1	2.9	6.5	Estonia, TAA 2611
5.30	3.84	1.38	21.2	6.2	3.4	6	Uzbekistan, TAA 104285
5.48	3.99	1.38	22.3	6.0	3.7	7	Uzbekistan, TAA 104436
5.51	4.07	1.36	21.2	5.9	3.6	7	Estonia, TAA 109781
5.01	3.87	1.30	17.7	5.9	3.0	7.1	Species mean
5%	4%	4%	11%	6%	12%	10%	CV

Phellinus laevigatus s. l.

4.28	3.31	1.30	16.6	5.7	2.9	7.5	Mean
15%	15%	6%	10%	9%	12%	11%	CV

Phellinus prunicola

5.21	3.95	1.32	20.8	4.5	4.6	6	USA, Michigan, MICH 22754-H
5.22	3.87	1.36	16.2	5.4	3.1	9.5	USA, Michigan, MICH Harper 1911
5.27	3.86	1.37	18.6	5.4	3.4	7	USA, Michigan, MICH Kauffman 1927
5.42	3.89	1.39	15.9	5.1	3.1	6	USA, New Hampshire, MICH Miller 25
5.71	4.38	1.30	18.5	7.1	2.6	7	USA, New York, PAC Overh. 1934
6.09	4.23	1.44	21.6	6.7	3.3	6	USA, Tennessee, TENN 8655
6.43	4.63	1.39	21.8	6.8	3.2	8	USA, Mississippi, TENN 16492

Phellinus rhamni

5.46	4.22	1.29	21.6	7,7	2.8	7	N. Caucasus, Chechnya, TAA 107819
5.53	4.27	1.30	24.5	8.4	2.9	6	Russia, Bryansk Prov., LE, **paratype**
5.66	4.82	1.17	23.8	8.1	2.9	6	Kazakhstan, LE, **holotype**
5.78	4.68	1.23	26.7	7.8	3.4	7	Austria, PRM 602329

Phellinus spiculosus

5.10	4.23	1.21	17.6	7.4	2.4	8.5	USA, Delaware, PAC Grassmeyr G46
5.12	3.88	1.32	15.8	5.4	2.9	5	USA, Maryland, MICH 22753
5.15	4.03	1.28	14.4	6.1	2.4	8.5	USA, Tennessee, PAC Hesler 3569
5.20	3.88	1.34	23.3	7.8	3.0	8.5	Canada, Ontario, TRTC 2294
5.27	4.59	1.15	18.1	6.5	2.8	6	USA, S. Carolina, SYRF 23623
5.36	4.10	1.31	20.1	7.6	2.7	6.5	USA, Texas, ARIZ 010517
5.55	4.88	1.17	17.9	7.5	2.4	8.5	USA, N. Carolina, PAC 450
5.61	4.71	1.19	16.0	7.0	2.3	7	USA, Missouri, PAC 639
5.65	4.64	1.22	18.7	6.7	2.8	7	USA, N. Carolina, PAC 10914
5.67	4.73	1.20	19.4	7.8	2.5	7	USA, Ohio, NY Morgan 298
5.69	4.91	1.16	15.4	5.7	2.7	6	USA, Indiana, PAC Bechtel 1933
5.71	4.74	1.20	21.0	6.7	3.1	7	USA, Ohio, PAC Cooke 1582
5.77	4.83	1.19	18.2	7.5	2.4	8.5	USA, Ohio, NY Morgan 75
5.81	4.85	1.20	18.9	7.9	2.4	6.5	USA, Ohio, NY Morgan 321
5.94	5.06	1.17	17.5	8.5	2.1	7	USA, Florida, NY Calkins
6.10	4.44	1.37	17.7	7.8	2.3	6.5	USA, Missouri, PAC 12267
5.54	4.53	1.23	18.1	7.1	2.6	7.1	Species mean
6%	9%	6%	12%	12%	11%	15%	CV

Phellinus sublaevigatus

5.12	4.11	1.25	32.1	6.3	5.1	6	New Zealand, PDD 5504